

1 **Reply to: Nutrient scarcity cannot cause mast seeding**

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3 **Authors:** M. Fernández-Martínez^{*1}, J. Sardans^{2,3}, F. Sayol^{4,5}, J.M. LaMontagne⁶, M.
4 Bogdziewicz⁷, A. Collalti^{8,9}, A. Hacket-Pain¹⁰, G. Vacchiano¹¹, J.M. Espelta³, J. Peñuelas^{2,3}, I.A.
5 Janssens¹

6 **Affiliations:**

7 ¹ Research Group PLECO (Plants and Ecosystems), Department of Biology, University of
8 Antwerp, 2610 Wilrijk, Belgium.

9 ² CSIC, Global Ecology Unit, CREAM-CSIC-UAB, Bellaterra 08193 Barcelona, Catalonia, Spain

10 ³ CREAM, Cerdanyola del Vallès, 08193 Barcelona, Catalonia, Spain

11 ⁴ Department of Biological and Environmental Sciences, University of Gothenburg, SE 405 30
12 Gothenburg, Sweden

13 ⁵ Gothenburg Global Biodiversity Centre, SE 405 30 Gothenburg, Sweden

14 ⁶ Department of Biological Sciences, DePaul University, Chicago, IL, USA

15 ⁷ Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University in Poznań,
16 Poland

17 ⁸ Institute for Agriculture and Forestry Systems in the Mediterranean, National Research Council
18 of Italy (CNR-ISAFOM), 87036, Rende (CS), Italy

19 ⁹ Department of Innovation in Biological, Agro-food and Forest Systems, University of Tuscia,
20 01100 Viterbo, Italy

21 ¹⁰ Department of Geography and Planning, School of Environmental Sciences, University of
22 Liverpool, Liverpool, UK

23 ¹¹ Università di Milano, DISAA. Via Celoria 2, 20133, Milan - Italy

24 * **Correspondence to:** M. Fernández-Martínez, marcos.fernandez-martinez@uantwerpen.be

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28 **Main text**

29 Kelly's commentary regarding our paper¹, claiming that nutrient scarcity cannot select
30 for masting behaviour in plants, initiated a fruitful discussion on traditionally settled
31 hypotheses about the evolution of reproductive behaviour in plants. In his commentary,
32 Prof. Kelly raises support for a contrasting hypothesis explaining our observation that
33 temporally variable seed production is more pronounced under nutrient scarcity,
34 namely that nutrient scarcity does not directly cause seed production variability, but
35 instead increases variability induced by economies of scale. The commentary hinges
36 mainly on the argument that an economy of scale (EOS) is necessary to select for
37 highly variable seed production. It also points out that there are no mechanisms by
38 which nutrient scarcity would select for that particular trait over generations. In reply to
39 the stimulating comment, we 1) propose a mechanism by which nutrient scarcity may
40 select for highly variable seed production, with weather patterns inducing masting
41 synchrony across populations; 2) further discuss why wind-pollination and predator
42 satiation, the EOS suggested by Kelly, cannot be the only selective pressures that
43 select for highly variable reproduction.

44 (1) There is robust empirical evidence^{2,3} showing that nutrient scarcity, and climate, are
45 long existing evolutionary forces that have selected for multiple plant traits and have
46 constrained the physiology of plants since their early development. Limiting resources,
47 such as water and nutrients, thus trigger the evolution of conservative traits for those
48 limiting factors³. Logically, nutrient availability is a direct determinant of the mean fruit
49 production in agriculture and in the wild⁴. In our paper¹, we hypothesised that low
50 nutrient availability is also an important factor selecting for highly variable and
51 synchronized seed production, the latter in combination with adaptation to variability in
52 long-term climate patterns. Our hypothesis as to why nutrient scarcity may have
53 selected for highly variable seed production in nutrient-poor plants, probably not
54 entirely explained in our original paper, was based on a mechanism linking highly

55 variable seed production in nutrient-poor plant species to increased inter- and
56 intraspecific competitiveness.

57 Because fruits are nutrient-enriched tissues⁵, their production under low fertility implies
58 a reduced allocation of nutrients to growth and defence⁶, and therefore lower
59 competitiveness and survival for the parent plants. Reductions in plant nutrient
60 concentrations after reproduction have been described for several species⁷, in addition
61 to growth and defence-reproductive trade-offs⁶. Therefore, when nutrients are scarce,
62 losing large amounts of nutrients year after year might jeopardize plant growth through
63 reduced photosynthesis, a highly nutrient-dependent process⁸. A constant yearly
64 reproduction would also imply a constant lowering of the availability of nutrients for
65 other processes. In contrast, nutrient accumulation in years with suitable weather
66 conditions for soil organic matter decomposition and mineralization may provide
67 sufficient nutrients to allow a high fruit crop in the following year, which would not come
68 at the expense of reduced competitiveness or increased mortality risk (**Figure 1**).
69 Under these conditions, high temporal variability would thus be beneficial and likely to
70 be selected for. In contrast, under nutrient-rich conditions, plants can potentially
71 reproduce regularly without jeopardising their competitiveness; this is actually one of
72 the reasons for fertilizer addition as a long-existing agricultural practice. This
73 mechanism, which could have originated during the early evolution of plants, may
74 explain why, under low nutrient availability, nutrient-conservative plants with highly
75 variable reproduction may have been preferentially selected in comparison to nutrient-
76 spending plants (with more constant reproduction). Further research including long-
77 term data sets of reproduction, growth and defence allocation, however, is still needed
78 to validate our hypotheses.

79 For a population to exhibit highly variable reproduction over time, a strong synchrony
80 among individuals is required⁹. Synchronous seed production is another important
81 feature of masting behaviour that has been traditionally associated with the benefits of

82 EOS, as it has been suggested to be an adaptive response to improve pollination
83 efficiency or escape seed predation⁷. Synchrony among individuals in a plant
84 population is the rule rather than the exception, as for example in leaf flushing, flower
85 blooming, die-back episodes or simply growth as shown by dendrochronology studies.
86 The most likely mechanism driving the synchrony in phenology, growth or reproduction
87 is the similar response of a population to changing weather patterns, by affecting
88 metabolism and plant resources.

89 Over time, the scientific community has discounted environmental effects based in part
90 on two assumptions that may not hold true, and this has fed the line of thought that
91 EOS benefits are necessary for high variable seed production to evolve. First, a direct
92 role of weather in synchronizing seed production has been discounted in part because
93 interannual variation in weather is much less than variation in seed production. We
94 argue that this line of argument does not hold because the link between weather and
95 seed production in a given year may be highly non-linear¹⁰. In Mediterranean regions,
96 for example, wet spring weather may simultaneously increase both carbon availability
97 through photosynthesis and nutrient availability through mineralization¹¹, boosting plant
98 resources and seed production. Second, proportional allocation has been assumed to
99 describe the passive allocation of resources to reproduction⁷. However, work in the
100 fields of ecological stoichiometry and carbon dynamics suggest that plants allocate
101 resources based on a hierarchy of needs, in which a set portion of resources goes
102 toward tissue maintenance at the expense of all other functions⁴. We, therefore,
103 suggest that interannual variability in reproduction is more likely to have been
104 evolutionary selected than synchrony.

105 (2) From evolutionary and theoretical bases, that highly variable reproduction can only
106 be selected because of wind pollination and predator satiation does not hold either. For
107 that to be true, we would have to accept that the common ancestors of plants, before
108 the trait of wind pollination and their seed predators evolved, did not show variable

109 seed production. In fact, it implies that the reproductive efforts of organisms other than
110 vascular plants, which do not produce pollen or may not have important predators of
111 their offspring, cannot be temporally variable unless, for other reasons, it evolved later
112 in these clades. However, there is evidence suggesting that other organisms that
113 reproduce sexually are also temporally synchronised and variable (**Figure 2**). Some
114 bryophytes tend to produce sporophytes more frequently than others¹², and their
115 production is mainly controlled by weather variability, like in vascular plants¹³, being
116 synchronised in time and space. The same happens with mushroom communities,
117 being highly synchronised, interannually variable, and highly dependent on weather
118 conditions¹⁴. Even the rates of animal fertility vary amongst years depending on the
119 amount of resources available, such as fertility rates of wild boars¹⁵. Given the fact that
120 temporally variable sexual reproduction in nature seems to be common, we should
121 conclude that factors others than wind pollination and predator satiation may have
122 played a role in shaping this reproductive trait. We suggest that one of these potential
123 factors triggering a highly variable seed production, before wind pollination and
124 predators evolved, may have been nutrient scarcity because of its role in determining
125 the physiology of a broad range of organisms³. Later on, wind pollination and predator
126 satiation may have evolved, reinforcing a highly variable seed production of vascular
127 plants. In order to better understand the evolutionary history of highly variable
128 reproduction in vascular plants, the field of masting will benefit from broadening its
129 scope and looking for inspiration in different disciplines and exploring examples from
130 other groups of organisms.

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171 **Correspondence and requests for materials should be addressed to:**

172 Marcos Fernández-Martínez: marcos.fernandez-martinez@uantwerpen.be

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174 **Conflict of interest**

175 The authors declare no conflict of interest.

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177 **Author contribution**

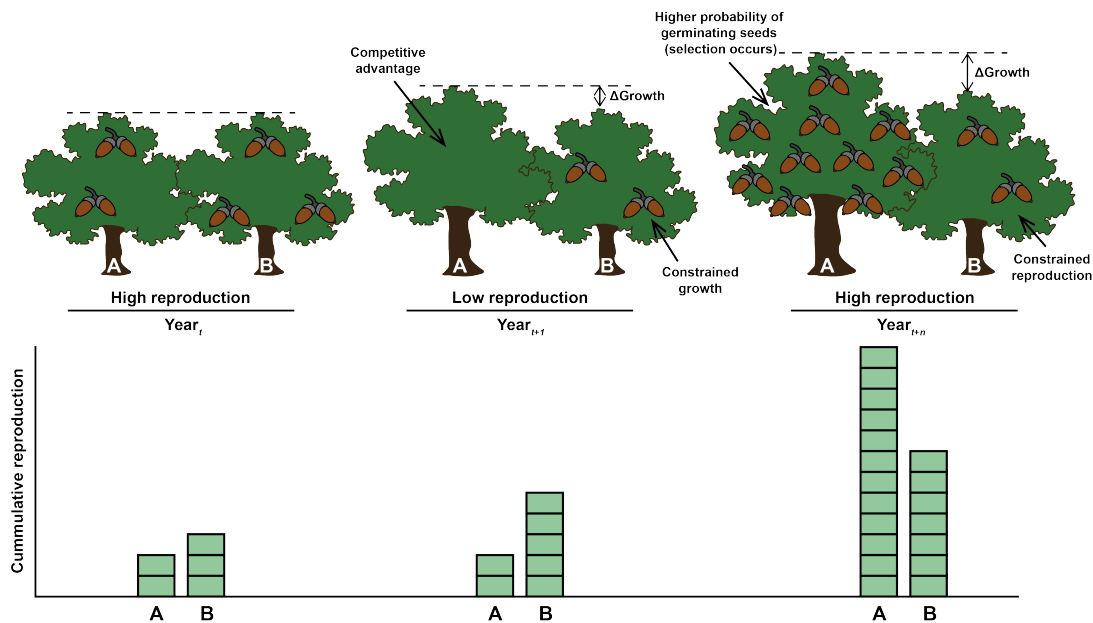
178 M.F-M., J.S., J.P., J.M.E., J.P. and I.A.J., conceived the paper. All authors contributed

179 equally to the writing of the manuscript.

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181 **Figure captions**

182 **Figure 1: Scheme showing the hypothesised mechanism by which nutrient**
183 **scarcity may act as a selective pressure of variable reproduction.** When nutrients
184 are scarce, delaying reproductive efforts may provide a competitive advantage given by
185 the lower rate of nutrient loss through reproductive structures. Losing nutrients through
186 reproduction may reduce growth in the short term by decreasing photosynthetic rates.
187 Under low nutrient availability, nutrient-conservative plants (A, with more variable
188 reproduction) outcompete, by vegetative growth, nutrient-spending plants (B, less
189 variable reproduction). This competition may thus increase the probability of seed
190 germination in nutrient-conservative plants and therefore potentially select for nutrient-
191 conservative traits such as high interannually variable reproduction. Synchronous
192 reproduction would then be the logical response to reproducing only when weather is
193 optimal and also selected for during evolution.



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196 **Figure 2: Four examples of interannually variable sexual reproduction.** (a)
197 Sporophytes of *Plagiomnium undulatum* (a species that produces sporophytes only
198 rarely); (b) acorn production by a *Quercus ilex* tree (often considered a *masting*
199 species); (c) mushroom production by *Hypholoma fasciculare* (fungal reproduction is
200 highly interannually synchronised within and across species); (d) a mother wild boar
201 with four piglets (sow fertility rates depend on the availability of food, such as acorns,
202 during *Quercus* mast years). The photographs in (a) and (b) were taken by Catherine
203 Preece, the photograph in (c) was taken by Jordi Corbera, and the photograph in (d)
204 was taken by M.F-M.

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